Biology and Biotype Determination of Greenbug, *Schizaphis graminum* (Hemiptera: Aphididae), on Seashore Paspalum Turfgrass (*Paspalum vaginatum*)

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ABSTRACT Greenbug, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae), was first discovered damaging seashore paspalum (*Paspalum vaginatum* Swartz) turfgrass in November 2003 at Belle Glade, FL. Inquiries to several golf courses with seashore paspalum turf across southern Florida indicated infestation was wide spread by April 2004. Damage symptoms progress from water soaked lesions surrounding feeding sites within 24 h to chlorosis and necrosis of leaf tips within 96 h. Problems caused by greenbug feeding were initially misdiagnosed as fertilizer, disease, other insects, or water management problems because aphids were not previously found on warm season turfgrasses. Greenbug development and fecundity studies were conducted on six seashore paspalum varieties: 'Aloha,' 'SeaDwarf,' 'SeaGreen,' 'SeaIsle,' 'SeaWay,' and 'SeaWolf.' Greenbug did not survive on 'SeaWolf.' Development rates (mean ± SEM) ranged from 7.6 ± 0.2 to 8.2 ± 0.2 d on the remaining varieties. Greenbug longevity and fecundity on 'Aloha' were significantly less than on the other varieties. The estimated intrinsic rate of natural increase (r_m) for greenbug ranged from 0.24 to 0.26 across tested varieties. Values for net reproductive rate (R_o) ranged from 12.3 on 'Aloha' to 40.4 on 'SeaWay.' In feeding trials on indicator plants, the Florida isolate of greenbug exhibited a unique biotypic profile most commonly found on noncultivated grass hosts. It was virulent on the wheat variety GRS1201 that is resistant to the principal agricultural biotypes attacking small grains and to all currently available resistant sorghum varieties.

KEY WORDS longevity, fecundity, net reproductive rate, instrinsic rate of natural increase

Seashore paspalum (*Paspalum vaginatum* swartz) is a warm season turfgrass gaining in popularity in tropical and subtropical areas of the world (Duncan and Carrow 2000). Its tolerance to saline irrigation water and soils, durability, and relative ease of maintenance has contributed to its popularity for use on athletic playing surfaces and commercial and residential lawns (Morton 1973, Duncan 1997). Greenbug, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae), was first discovered damaging the warm season turfgrass seashore paspalum (cultivar SeaDwarf) in November 2003 at the University of Florida's Everglades Research and Education Center, Belle Glade, FL (Nuessly et al. 2004). Greenbug infestations have now been observed on *P. vaginatum* turfgrass golf courses and sod farms in central and southern Florida (Nuessly and Nagata 2005a).

The greenbug is a worldwide pest of Graminaceous plants, particularly small grains, in North, Central, and South America, Europe, Africa, the Middle East, and Asia (Blackman and Eastop 2000). The first North American report of this aphid was on wheat and barley in Virginia in ≈1882 (Webster and Phillips 1912). Greenbug was reported feeding on bluegrass turfgrass in Washington, DC, as early as 1909 (Bowed 1983). In early 1968, a biotype that caused severe damage to grain sorghum became common in Nebraska and soon spread throughout grain-producing areas of North America (Harvey and Hackerott 1969). Nine greenbug biotypes that damage small grains have been identified (Porter et al. 1997). Greenbugs are known to infest native North American grasses and introduced cool season turfgrass species, especially bluegrass and other *Poa* species (Dahms et al. 1954, Street et al. 1978, Bowed 1983, Michels 1986, Kindler and Hays 1999). Greenbug alata have been regularly collected in suction traps located across the Florida peninsula since a trapping study began in 1998 (Halbert and Nuessly

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Table 1. Mean (±SEM) development, longevity, and fecundity of greenbugs feeding on several varieties of seashore paspalum

Variety	Origin	*n*	Development (d)		*n*	Longevity (d)		*n*	Fecundity		r_m	R_o
Aloha	Hawaii	9	8.2 ± 0.2a		10	16.4 ± 2.8a		12	14.6 ± 2.7a		0.235	12.3
Sea Dwarf	Florida	11	7.6 ± 0.2a		11	26.5 ± 2.7b		12	38.3 ± 3.7b		0.255	35.3
Sea Green	Florida	10	7.9 ± 0.2a		11	24.9 ± 2.7b		12	34.0 ± 4.1b		0.239	30.8
Sea Isle	Argentina	12	8.2 ± 0.2a		12	25.2 ± 2.5b		12	29.1 ± 3.8b		0.240	29.1
Sea Way	Florida	8	7.7 ± 0.2a		8	30.1 ± 3.1b		12	38.4 ± 6.0b		0.262	40.4
	ANOVA	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*		
	Variety	4,35.062	1.75	0.1613	4,38.412	3.38	0.0183	4,44	2.61	0.0484		
	Replicate	11,34	0.63	0.7868	11,36	1.69	0.1145	11,44	1.94	0.0599		

Anova conducted using PROC MIXED (SAS Institute 2003). Means in the same column followed by different letters are significantly different; *t*-test ($P < 0.05$).

2004), but they were not found feeding on seashore paspalum turfgrass until late in 2003.

Schizaphis graminum damages plants by feeding and through virus transmission. Greenbug saliva has enzymatic activity that breaks down cell walls and chloroplasts in susceptible plants (Al-Mousawi et al. 1983). Plant viruses transmitted by greenbug include barley yellow dwarf (Murphy 1959), sugarcane mosaic (Ingram and Summers 1938), and maize dwarf mosaic (Nault and Bradley 1969).

Greenbug causes characteristic damage to seashore paspalum (Nagata et al. 2005, Nuessly and Nagata 2005a), but symptoms can be initially confused with disease, water, or fertilizer problems. The aphid feeds and reproduces on leaves and stems but prefers locations along the midrib of the upper leaf surface on this turfgrass. Initial feeding results in small yellow chlorotic spots surrounded within 24 h by rings of water-soaked tissue. Within a few days the spots enlarge, become brighter yellow, and coalesce with other feeding spots. Four days after initiation of feeding, infested leaves develop brown necrotic leaf tips. A bright yellow band separates necrotic and living leaf tissue. Aphids vacate heavily damaged, chlorotic leaf areas in favor of green leaf tissue. Turfgrass damage spreads outward from initial infestation loci as aphid colonies move to more acceptable foliage. Heavily damaged patches of turfgrass appear thin or sparsely planted with little green tissue. Greenbugs feeding on seashore paspalum do not produce noticeable amounts of honeydew; hence, leaves do not get sticky nor serve as a substrate for sooty mold growth. Initial studies with greenbug on seashore paspalum focused on chemical control of greenbug on turfgrass (Nuessly and Nagata 2005b) and host plant resistance (Nagata et al. 2005). The purpose of this work was to examine the biology and biotype of greenbug associated with seashore paspalum turfgrass.

Materials and Methods

Aphid and Plant Culture. All greenbugs used in these experiments were from a colony established at the Everglades Research and Education Center (EREC) from individuals collected from naturally infested seashore paspalum grown outdoors at Belle Glade, Palm Beach County, FL. Greenbugs were maintained on ≥14-d-old USU-Apogee wheat plants (*Triticum aestivum* L.) growing in Fafard 2 planting medium (Conrad Fafard, Agawam, MA) in a laboratory growth room where temperature was minimally controlled (range, 18–25°C). Artificial lighting was provided using cool white fluorescent tubes on a 14:10 (L:D)-h photoperiod. Eight to 10 wheat seeds were planted in each pot, and plants were fertilized and watered as needed to ensure proper growth. Greenbugs were transferred to new wheat plants weekly by clipping infested leaves and placing them in contact with the new plants.

Plants for biology studies were established using sprigs cut from six varieties of seashore paspalum grown outdoors at the EREC. Varieties tested were 'Aloha,' 'SeaDwarf,' 'SeaGreen,' 'SeaIsle,' 'SeaWay,' and 'SeaWolf.' These varieties originated from cuttings collected in Hawaii and Florida in the United States and in Argentina (Table 1). Two sprigs were set into 6 by 6 by 8-cm pots (l by w by h) containing Fafard 2 planting medium. Plants were placed on a greenhouse mist bench for 14 d to aid rooting and plant establishment, after which they were moved to an environmentally controlled greenhouse where they were maintained.

Aphid Biology. An experiment was conducted to determine greenbug developmental time (nymph to first reproduction), longevity (birth to death), and fecundity on seashore paspalum turfgrass. Plants were naturally infested with nymphs by placing mixed age alata randomly selected from the colony onto plants for 4–48 h. Adults were removed after two nymphs were produced and had settled to feed. All adults were removed after 2 d whether or not nymphs were produced. Experimental units consisted of individual plants containing one or two nymphs. Plants were caged individually within 2-liter, ventilated cages made from two transparent plastic food service containers (11 cm diameter by 13 cm deep; Berry Plastics, Evansville, IN) joined at their openings. A hole was cut out of two removable lids leaving only the ring seals. The two ring seals were glued together and served as the connector between the two containers. The bottom of the uppermost container was removed and replaced with a fine mesh cloth for ventilation. The experiment was conducted in a plant growth room with artificial light at 14:10 (L: D)-h photoperiod

Table 2. Results of biotype determination tests with Florida isolate of greenbug

Plant resistance source[a]		Resistance source (gene)	Biotypes										Florida isolate
			A	B	C	E	F	G	H	I	J	K	
Wheat	Custer	Susceptible check	S	S	S	S	S	S	S	S	**R**	S	S
Wheat	DS 28A	*Gb1*	**R**	S	S	S	**R**	S	S	S	**R**	S	**R**
Wheat	Amigo	Gb2		**R**	**R**	S	S	S	S	S	**R**	S	**R**
Wheat	Largo	Gb3		S	**R**	**R**	S	S	**R**	**R**	**R**	**R**	S
Wheat	CI 17959	*Gb4*		S	**R**	**R**	S	S	S	**R**	**R**	**R**	S
Wheat	CI 17882	*Gb5*		S	**R**	**R**	S	S	S	**R**	**R**	**R**	S
Wheat	GRS 1201	*Gb6*		**R**	**R**	**R**	S	**R**	S	**R**	**R**	**R**	S
Rye	Elbon	Susceptible check		S	S	S	S	S	S	S	**R**	S	S
Rye	Insave	*Gb2, Gb6*		**R**	**R**	**R**	S	**R**	S	**R**	**R**	**R**	**R**
Barley	Wintermalt	Susceptible check		S	S	S	S	**R**	S	S	**R**	S	S
Barley	Post 90	Rsg1a		**R**	**R**	**R**	**R**	**R**	S	**R**	**R**	**R**	**R**
Barley	PI 426756	*Rsg2b*		**R**	**R**	**R**	**R**	**R**	S	**R**	**R**	**R**	**R**
Sorghum	TX 7000	Susceptible check		—	S	S	—	S	—	S	—	S	S
Sorghum	TX 2737	—		—	**R**	S	—	S	—	S	—	S	S
Sorghum	TX 2783	—		S	**R**	**R**	S	S	—	S	—	S	S
Sorghum	PI 550607	—		**R**	**R**	**R**	S	**R**	**R**	**R**	—	S	S

[a] Data from Wood (1961), Harvey and Hackerott (1969), Teetes et al. (1974), Johnson et al. (1982), Porter et al. (1982), Peterson et al. (1984), Kindler and Spomer (1986), Puterka et al. (1988), Harvey et al. (1991), Andrews et al. (1993), Beregovoy and Peters (1995), Harvey et al. (1997), and Peters et al. (1997).

R, plant source resistant to greenbug feeding (plants survive); S, plant source susceptible to greenbug feeding (plants die).

and temperature ranging from 18 to 26°C. Cages were removed from the growth room and inspected daily between 0830 and 1200 hours for aphid development, nymph production, and mortality of F_1 adults. After reproduction began, newly produced nymphs were removed daily. The intrinsic rate of natural increase (r_m) for apterous aphids was estimated using the formula proposed by Wyatt and White (1977) for aphids: $r_m = 0.738\ (\log_e M_d)/d$, where d is the number of developmental days from birth to first reproduction, and M_d is the mean number of progeny produced in the reproductive interval equal to d. The net reproductive rate (R_o) for greenbug on seashore paspalum was calculated using the equation $R_o = \sum l_x m_x$, where l_x is the proportion of living females on a given day, and m_x is the mean number of female births on that day (Southwood 1978). All nymphs produced by individuals of this viviparous colony were considered to be females.

Proc mixed (SAS Institute 2001) was used to analyze the data because of the presence of both fixed and random effects in the experimental designs. Variety was modeled as a fixed effect, whereas replicate and variety × replicate were modeled as random effects. Analysis of variance (ANOVA) was conducted using the type 1 method because of unequal sample sizes. SAS calculated the degrees of freedom using the containment method. The lsmeans statement was used to generate SEs for the means, and the pdiff command was used to perform *t*-test comparisons of the least square means.

Biotype Determinations. Tests to determine the biotypic status of greenbugs from this new plant–insect interaction were conducted at the USDA–ARS, Wheat, Peanut, and Other Field Crops Research Laboratory in Stillwater, OK. Greenbugs from a 3-mo-old colony at EREC were placed within sealed 15-cm-diameter petri dishes, packed with cool packs in a Styrofoam cooler, and shipped to the USDA facility using overnight service. Test colonies were established and maintained on 'Schuyler' barley (*Hordeum vulgare* L.) seedlings that were enclosed within ventilated clear plastic cylinders. Biotypic evaluation was conducted using three clonal test colonies that were established from individual, apterous greenbugs. Test colonies were reared on Schuyler barley grown in caged pots and maintained in environmental chambers with a photoperiod of 16:8 (L:D) h at 20 and 18°C, respectively.

The biotypic status of each test colony was determined using previously established plant differentials of wheat, rye (*Secale cereale* L.), barley, and sorghum (*Sorgum bicolor* L. Moench) (Starks and Burton 1977) (Table 2). Seeds of each differential plant entry were planted in individual rows, at a rate of 10 seeds per 15-cm row to fritted clay soil-less planting media (Absorb-N-Dry; Balcones Minerals, Flatonia, TX) in greenhouse flats. Plant entries were randomly assigned to rows and the experiment was replicated four times. Wheat, rye, and barley plants were tested separately from sorghum. Before testing, each greenbug test colony was increased to ensure an adequate aphid population for testing. Immediately after planting, the flats containing the test plants were caged to ensure that invasive aphids would not contaminate the plants. The caged plants were infested at the two-leaf stage by cutting and placing infested leaves next to each row of test plants. The wheat, rye, and barley tests were conducted in a greenhouse, under artificial light, with a photoperiod of 16:8 (L:D) h, at 22 ± 5°C. The conditions for the sorghum tests were the same except for the temperature, which was maintained at 28 ± 5°C. Once the susceptible control plants ('Custer' wheat, 'Elbon' rye, and 'Wintermalt' barley) were killed, the test was terminated, and the plants were scored as alive (resistant) or dead (susceptible). After the test, aphid vouchers were collected and deposited at the Cereal Insect Genetic Resource Library,

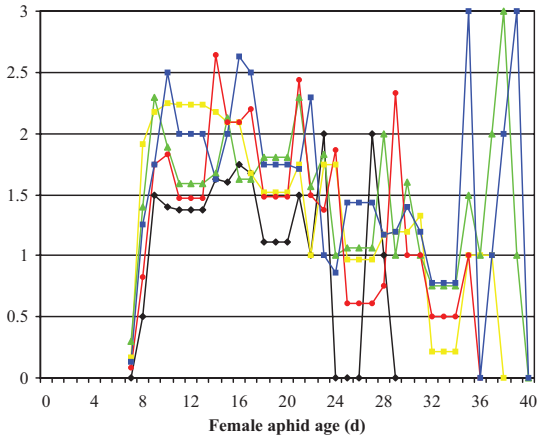

Fig. 1. Mean number of greenbug aphid progeny per day for five seashore paspalum varieties. 'Aloha,' black diamonds; 'SeaDwarf,' yellow squares; 'SeaGreen,' green triangles; 'SeaIsle,' red circles; 'SeaWay,' blue squares.

USDA–ARS, Plant Science Research Laboratory, Stillwater, OK.

Results

Aphid Biology. Variety affected the development and longevity of *S. graminum* on seashore paspalum. SeaWolf was not a suitable host for greenbug. Adults usually moved off SeaWolf within an hour of placement on the variety. The few nymphs produced on this very coarse selection failed to complete development. Therefore, results for greenbug on SeaWolf were not included in Table 1. There was no significant difference in development rates among the remaining five varieties (Table 1), and only a single nymph died before reaching the adult stage on these varieties. Development rates (mean ± SEM) ranged from 7.6 ± 0.2 to 8.2 ± 0.2 d. Greenbugs lived from 6 to 42 d on seashore paspalum, with those on Aloha living significantly fewer days (≥8 d) than on other varieties.

Greenbug fecundity also was significantly affected by variety on seashore paspalum (Table 1). Fecundity was significantly less on Aloha (on which nymph production was ≥50% less than on the other varieties). Greenbug prereproductive period was not strictly measured, but ≈33% of the F_1 aphids started nymph production within 3 h of molting into the adult stage, and all had produced nymphs within 24 h. Mean daily nymph production ranged from 0 to 3/d (Fig. 1). Mean daily nymph production first fell below 1/d 16 d after reaching the adult stage on Aloha and SeaWay and after 17 d for SeaIsle. Females frequently continued to produce nymphs until their deaths, even >30 d after reaching adulthood. Although no nymphs were produced on Aloha after 21 d, nymph production continued to 39 d on SeaGreen and SeaWay. Nymph production across varieties ranged from 6 to 69 per female, with a mean of 34.6 ± 2.2 (n = 49).

Statistics on the potential growth of a greenbug population on seashore paspalum turfgrass were calculated from results of our growth room experiments. The estimated intrinsic rate of natural increase (r_m) for greenbug was very similar on the five varieties and ranged from 0.24 to 0.26. However, variety appeared to have a large effect on the net reproductive rate (R_o) for greenbug. Values for R_o ranged from 12.3 on Aloha to 40.4 on SeaWay (Table 1).

Biotypic Determination. The phenotypic profiles of the Palm Beach County Florida greenbug isolate and the nine documented biotypes are shown in Table 2. The Florida isolate exhibited a unique biotypic profile, which was most similar to the profiles of biotypes B and F, matching 12 of 14 susceptible-resistant reactions. Biotype G also was similar to the Florida isolate matching 11 of 16 reactions. Biotypes F, G, and H are not typically found on cultivated grain crops but are found on noncultivated grass crops. Moreover, the Florida isolate was virulent to GRS1201 wheat, which is resistant to the principal agricultural biotypes (C, E, I, and K) that are currently found attacking small grains and sorghum crops in the United States. When tested against sorghum lines, the Florida isolate was virulent to all currently available resistant varieties.

Discussion

Published records of biological indices of various greenbug isolates at temperatures similar to those used in our study on crop and noncrop plants provides for at least informal comparison with those of the Florida isolate. A prereproductive period <1 d between molting to the adult stage and first nymph production was also observed by Wadley (1931) for greenbug on oats (*Avena sativa* L.). Biotypic isolates were not distinguished in papers published before ≈1961. The detailed results of Wadley (1931) of greenbug biology indicate faster development, longer reproductive period, and higher fecundity on oats than for the Florida isolate on seashore paspalum. Similar elevated biological indices compared with the Florida isolate were found for the following greenbug biotypes on susceptible crop varieties: B on wheat (Wood 1961); A, B, and C on barley (Wood and Starks 1972); and B, C, E, and F on grain sorghum (Kindler and Spomer 1986). Biotype E also displayed faster development and higher r_m on susceptible wheat, grain sorghum, barley, rye, and oats than the Florida isolate on seashore paspalum (Kerns et al. 1989). However, the r_m for the Florida isolate was higher than for biotype E on greenbug-resistant wheats (Webster and Porter 2000, Lage et al. 2003).

Reported greenbug biological indices on pasture, noncrop, and cool season grasses were mostly lower than those for the Florida isolate in our study. Greenbug fecundity was higher on only 1 (jointed goat grass, *Aegelops cylindrica* Host.) of 23 grass species tested by Dahms et al. (1954) than for the Florida isolate on *P. vaginatum.* They were unable to sustain a greenbug population on the pasture grass smoothseed paspalum, *Paspalum pubiflorum* variety *glabrum* Vasey. This was the case with our studies on the *P. vaginatum* variety SeaWolf where adults rarely settled on plants and

none of the nymphs survived. Nymph production was higher for the Florida isolate on *P. vaginatum* than for members of a greenbug population collected from South Dakota grasses and placed on 10 range grass (Stoner and Kieckhefer 1979) and 14 *Agropyron* species (wheatgrass) (Kieckhefer 1983). Fecundity of the Florida isolate was higher than those reported for biotypes B, C, E, F, G, H, I, and K on the cool season grasses *Agropyron cristatum* L. Gaertner, *A. desertorum* (Fischer ex Link) Schultes, *Bromus catharticus* Vahl, *B. inermis* ssp. *inermis* Leysser, *B. marginatus* Nees ex Steudel, *Pascopyrum smithii* (Rydberg) A. Love, and *Poa compressa* L. (Kindler and Hays 1999).

Significant differences in biological indexes among the six tested varieties of seashore paspalum indicate there are possible antixenotic and antibiotic mechanisms for resistance to greenbug in *P. vaginatum.* The pubescent stems and leaves of SeaWolf may present a physical barrier that reduced settling and successful development. Reduced longevity and fecundity on Aloha would slow the development and spread of this aphid and thereby increase the chance for predation and parasitism. This work has only scratched the surface of the available *P. vaginatum* germplasm. Additional greenbug resistant germplasm may exist that have the desirable agronomic characters of Aloha (e.g., fine leaf blades) with the level of resistance exhibited by SeaWolf.

Thus far, all reports of greenbug infestation have been on small grain and sorghum crops, cool season turfgrasses, and some native North American grasses. Before 2003, no warm season turfgrass species had been reported with a greenbug infestation. Should we consider the green bug infestation of seashore paspalum an anomaly or should we be looking for and preparing for more discoveries of this type involving other warm season turfgrass species? In light of research reported here and based on the history of cool season grasses, the greenbug should be considered an emerging problem for seashore paspalum and other warm season turfgrasses (Vittum et al. 1999). Greenbugs have been a sporadic pest of Kentucky bluegrass since the early 20th century, but it was not until the 1970s when they became a regular and recurring problem of bluegrass lawns. In addition, greenbugs have been reported to develop insecticide resistance, making their control more difficult (Niemczyk and Moser 1982, Porter et al.1982).

Greenbug biotypes have been generally defined as infraspecific populations that are able to injure a select group of plants containing specific resistant gene(s) that are resistant to other infraspecific populations. Accordingly, as more resistant genotypes were developed, new biotypes were discovered. Consequently, a gene-for-gene model was assumed, whereby newly developed resistant varieties putatively exerted selective pressure on the current predominant biotype, which in turn lead to the development of a new virulent biotype. However, genetic evidence confirms that the divergence of greenbugs into biotypes predates the development of all plant resistant hybrids (Shufran et al. 2000, Anstead et al. 2002). Therefore, greenbug biotypes had to have originated on noncultivated grass hosts. Because greenbugs have a wide host range and a great potential for numerous host races (Michels 1986), the discovery of the Florida isolate virulent on cultivated *P. vaginatum* is not surprising.

Plant resistance is a cost effective and environmentally sound pest management component that will continue to be an important tool for mitigating insect damage. The discovery of the Florida isolate shows the need for developing a plant screening strategy to assess the biotypic variation of endemic greenbug populations and to identify resistant germplasm for future *P. vaginatum* varietal development.

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